4.—Skull and tooth variation in Australian bandicoots (Peramelidae, Marsupialia): the genus Isoodon and multivariate comparisons with Perameles

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Abstract

The morphological and metrical features of the skull and teeth of certain taxa of the genus *Isoodon* are described and analysed. Multivariate comparisons are then made between these and a number of *Perameles* taxa. The main multiple discriminant analyses, using either cranial or dental features alone, achieve good separation of the genera (principally on the 1st function), and of the lower taxa within each genus (mainly by the 2nd function).

Introduction

This study is part of an ongoing investigation being made of skull and tooth variation in the bandicoots (Peramelidae: Marsupialia) of Australia. In a series of previous studies (Freedman, 1967; Freedman and Joffe 1967a and b), the anatomical and metrical features of the skull and teeth of species of the genus *Perameles*, the long-nosed bandicoots, were reported on. The present study utilises material from the major United States collections to examine the variations of the same features in certain species of the genus *Isoodon*, the short-nosed bandicoots. The main sample is of *I. macrourus*. In addition multivariate comparisons are made of the cranial and dental features of a number of taxa of *Isoodon* and *Perameles*. The usefulness of multivariate discriminant analysis in taxonomic studies is again apparent.

Taxonomy of Isoodon

In most of the recent classifications of the genus *Isoodon* nine taxa are recognised. Thus, Tate (1948) and Marlow (1962) both list three species in the genus, the first two species each including a number of subspecies. The species they list are: *I. obesulus* (with 6 subspecies), *I. macrourus* (with 2 subspecies) and *I. barrowensis* (monotypic). For the same genus, Troughton (1957) delimits nine similar groups, but he describes *I. obesulus* as comprised of 3 subspecies and he regards the remaining 6 taxa as each being of full specific rank.

In the present study, a classification and distribution ranges similar to those outlined by Tate (1948) and Marlow (1962) will be used (Fig. 1). Thus, *I. obesulus* includes *I. o. obesulus* (southern half of coastal New South Wales, most of Victoria and an adjacent coastal portion of South Australia), *I. o. affinis* (Tasmania), *I. o. nauticus* (2 islands in the Nuyts Archipelago off the coast of South Australia), *I. o. fusciventer* (south west part of Western Australia), *I. o. auratus* (north east part of Western Australia and adjacent Northern Territory) and *I. o. peninsulae* (northern tip of Queensland). The species *I. macrourus* includes *I. m. macrourus* (northern part of Northern Territory) and *I. m. torosus* (east coast of Queensland and north half of the coast of New South Wales). The third species is *I. barrowensis* and its locality is Barrow Island, off the north west coast of Western Australia.

Materials and Methods

The samples of the genus *Isoodon* assembled for the present study total 77 individuals and are from collections in the United States of America. They were kindly made available to us by the American Museum of Natural History and the Archbold Expeditions, New York (Dr. Hobart M. van Deusen), the Field Museum of Natural History, Chicago (Dr. William D. Turnbull) and the Smithsonian Institution, Washington (Dr. Henry W. Setzer). This material includes 24 specimens of *I. m. macrourus* (15 males and 9 females) and 38 specimens of *I. m. torosus* (24 males and 14 females). The sexes of a few of the *I. m. torosus* individuals were not recorded, and (on criteria discussed below) they were sexed on morphology and size. The number of *I. obesulus* specimens is only 14, and of these there are only 6 known males and 3 known females. The sample of this species includes individuals of *I. o. obesulus*, *I. o. affinis*, and *I. o. fusciventer*, but, because of the very small numbers, no attempt was made to treat these subspecies separately. Of *I. barrowensis* there is only a single specimen (Smithsonian Institution No. 218462). The whole of the available sample has been utilized for the morphological description and univariate analysis of *Isoodon*.

The main multivariate statistical tool used for comparing taxa was discriminant function analysis. Various aspects of the principles and methodology of the technique will be dealt with in the course of describing and discussing comparisons and results. Computation of the discriminants here reported was carried out at the University of Wisconsin Computer Center using a slightly modified version of program EIDISC (distributed by the Vogelback Computing Center, Northwestern University). This program provides output similar to that discussed in chapters 6 and 7 of Cooley and Lohnes (1962).

For the multivariate analyses utilizing the *Isoodon* data, the numbers in the various taxa had to be slightly reduced (Table 8) due to cer-

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tain of the specimens being either immature or damaged. The *Perameles* samples used in those tests (175 individuals) were described in Freedman (1967). The measurements, aging and sexing criteria, and the general methodology utilised in the present study, are outlined in Freedman and Joffe (1967a).

Skull and dental morphology in Isoodon

A fairly detailed morphological description, including drawings and photographs, was given by Freedman (1967) of the skull and dental features of *Perameles nasuta*. In that same study, the morphological variations of *P. gunnii* and *P. bougainville* from the *P. nasuta* description were also outlined, and standard view photographs of these two species were included in that and two subsequent papers (Freedman and Joffe, 1967a and b). The basic *P. nasuta* description very largely also holds for the genus *Isoodon* and, in the present study, only a series of standard view photographs and brief notes highlighting the important differences of the various *Isoodon* taxa to the *P. nasuta* description will be given.

(a) *I. macrourus*:—The skull of *I. macrourus* (Fig 2, *I. m. macrourus*) is very much more robustly constructed in all respects than that of *P. nasuta*. The bone is generally thicker and the muscle markings are far more prominent. The length of the *I. m. torosus* cranium is, on average, almost as great as that of *P. nasuta*, but the mean cranial length of *I. m. macrourus* is rather less than in that species, the decrease in the females being less marked than in the males.

Compared to *P. nasuta*, the cranial breadth and height dimensions appear to be absolutely greater in *I. m. torosus*, but only relatively greater in *I. m. macrourus*. Notable amongst the differences in overall shape of the cranium is the greater relative muzzle breadth in both subspecies of *I. macrourus* which makes the muzzle appear relatively shorter and less attenuated distally than in *P. nasuta*. It is mainly this feature which gives the genus *Isoodon* its popular name of short-nosed bandicoots.

In the palate the posterior palatine vacuities of *I. macrourus* are rather smaller than those in *P. nasuta* and the premaxillae do not project anteriorly as far beyond the incisors as they do in that form. Perhaps the two most marked cranial differences between *I. macrourus* and *P. nasuta* are the more heavily built zygomatic arches and, on the undersurface of the cranium, the very greatly inflated alisphenoid bullae in the former species. In the mandible of *I. macrourus* the coronoid process, and in fact the whole of the ascending ramus, is particularly broad in an antero-posterior direction. Also, the ramus is more nearly at right angles to the body than in *P. nasuta* and this feature is more marked in *I. m. macrourus* than in *I. m torusus*.

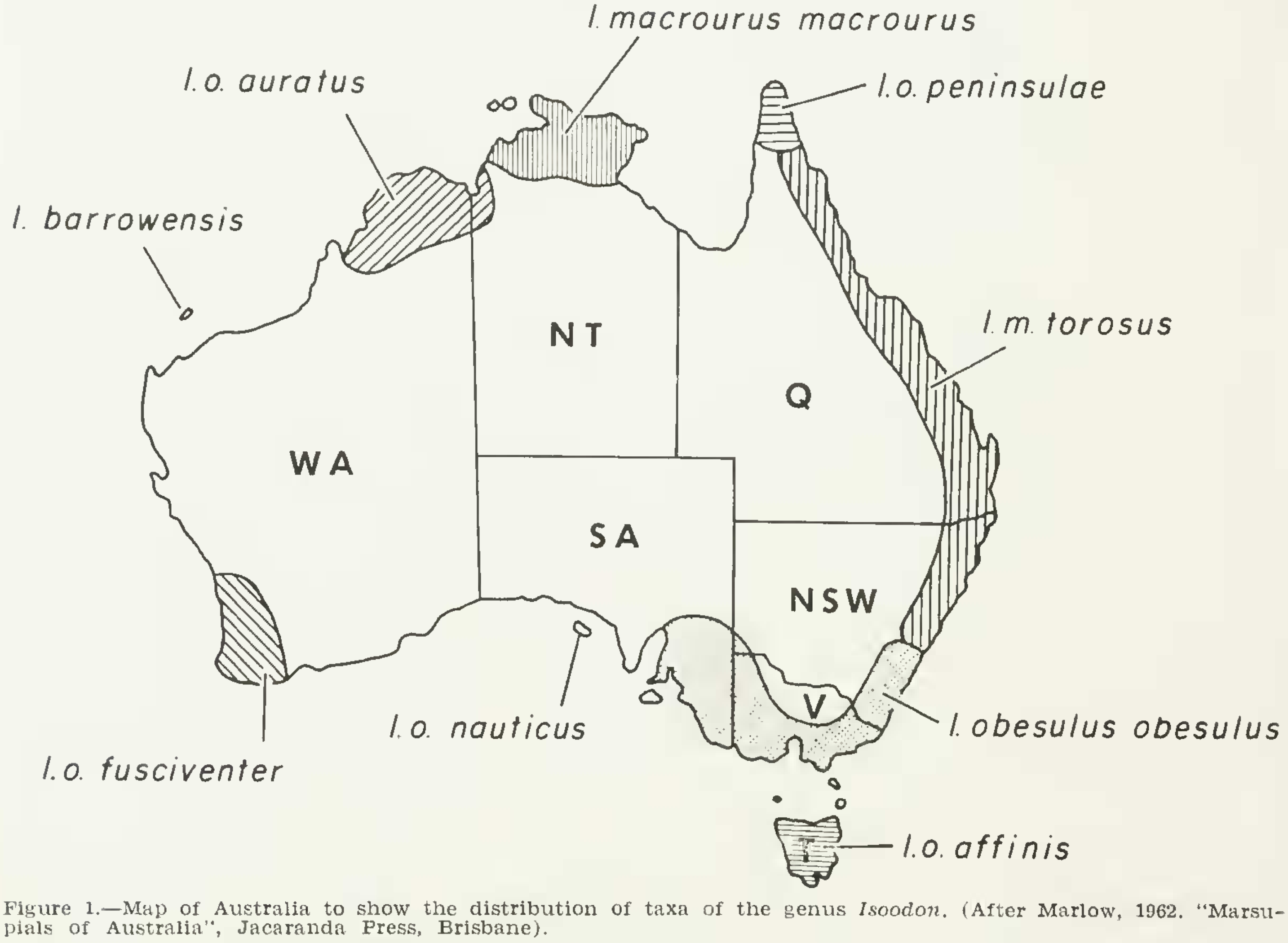

Figure 1.—Map of Australia to show the distribution of taxa of the genus *Isoodon*. (After Marlow, 1962. "Marsupials of Australia", Jacaranda Press, Brisbane).

The individual teeth of *I. macrourus* are considerably larger than those of *P. nasuta*, with the exception of I^1 which is a particularly small tooth. The molar teeth are also more square in *I. macrourus* and in the upper molars the disto-buccal corner is not elongated distally as in *P. nasuta*. In addition the last premolar in *I. macrourus*, especially the upper tooth, is a particularly broad and robust tooth.

Sexual dimorphism in the skull and teeth of *I. m. torosus* appears to be restricted to size differences in most of the skull dimensions and tooth row lengths, the canine tooth dimensions and, of the single other teeth, mainly in measurements of M4. The morphological sex difference in the canine teeth described in *Perameles* species does not appear to be consistently present in *Isoodon*. In *I. m. macrourus*, except in canine size, there was little evidence of sexual dimorphism in the skull or teeth.

(b) *I. obesulus*:—In the other species of *Isoodon* for which a fair sample is available, *I. obesulus*, the skulls are considerably smaller than in *P. nasuta* and rather more similar in size to *P. bougainville*. The male individual shown in Figure 3 *(I. o. affinis)* is the largest specimen of *I. obesulus* measured. Although very much smaller in size, the overall shape of *I. obesulus* is very similar to that of *I. macrourus* and it also shows the very greatly inflated bullae characteristic of the genus *Isoodon*.

In the structure of the palate, *I. obesulus* is different to *P. nasuta* and also to *I. macrourus*, but shows resemblance to both *P. gunnii* and *P. bougainville*. As in those species, between the anterior and posterior palatine vacuities there is an additional pair of fairly large antero-posteriorly elongated vacuities, and posterior to the posterior pair, which are large, there is a scattered group of vacuities lying close to the posterior end of the palate. In the mandible, the angle of the ascending ramus to the body is more obtuse than in *I. macrourus*, however, the ramus is antero-posteriorly broad as in that species.

In the dentition, the molars of *I. obesulus*, like those of *I. macrourus*, appear more compact than those of *P. nasuta*, and, especially in the upper jaw, the teeth show evidence of being more crowded than in either *P. nasuta* or *I. macrourus*. P^3 is similar to the equivalent tooth

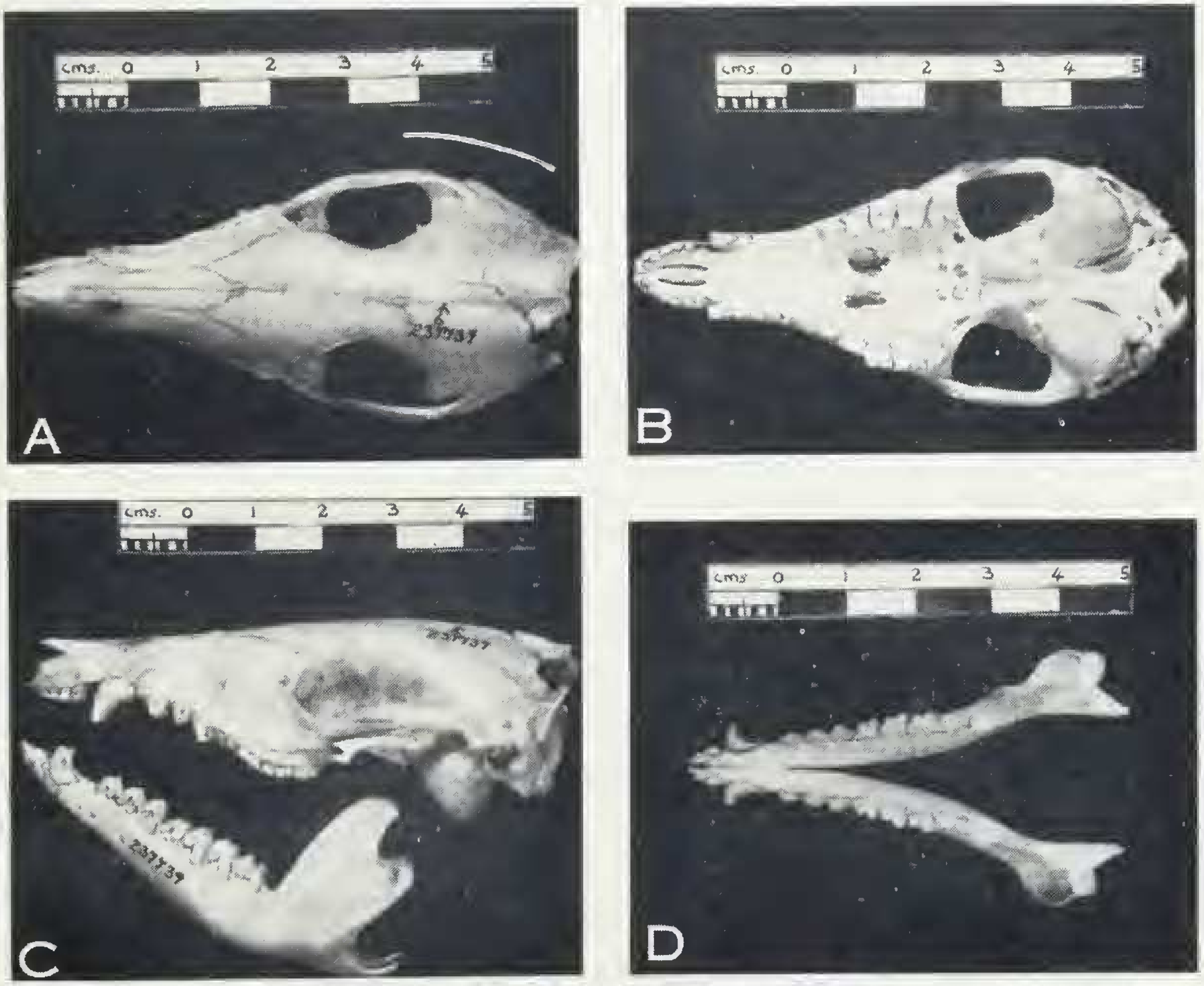

Figure 2.—*Isoodon macrourus macrourus* male (Smithsonian Inst. No. 237739). A.—dorsal view of cranium; B.—ventral view of cranium; C.—lateral view of cranium and mandible; D.—occlusal view of mandible.

TABLE 1

Comparison of Isoodon m. torosus *male and female skull measurements (in mm)*

Measurement	Males			Females			" t "
	N	$\bar{X}$	VAR.	N	$\bar{X}$	VAR.	
Cranium							
(a) length—							
Max.	18	84·74	42·24	7	74·62	18·34	3·786**
Bas.	18	75·92	25·81	7	67·72	12·37	3·897**
Cond.-Bas.	18	79·78	26·06	7	70·98	16·27	4·074**
Pal.	18	49·71	11·05	8	45·03	7·19	3·496**
Nas.	18	33·88	10·69	6	31·11	6·61	1·880n.s.
Fr. ..	18	25·64	7·17	7	21·55	2·01	3·804**
Par.	18	22·16	5·68	7	19·72	2·83	2·465*
Ant. to I^1	16	2·13	0·05	7	1·98	0·02	1·626n.s.
(b) breadth—							
Ant. to C	18	9·42	0·49	8	8·03	0·31	4·945**
at M^2 ...	18	23·76	2·35	8	21·47	1·09	3·827**
Int.-Orb.	18	22·66	2·32	8	20·21	0·40	4·346**
Min. Fr.	18	11·81	0·30	7	11·65	0·20	0·686n.s.
Bizyg.	18	37·31	7·15	7	31·94	2·72	4·924**
Cran.	18	27·34	3·09	7	24·65	1·75	3·648**
(c) height—							
Ant. to C	17	7·35	0·34	8	6·15	0·12	5·356**
Post. to M^4	18	20·37	1·11	8	18·23	0·40	5·300**
Cran. ..	18	27·83	2·21	7	25·32	0·93	4·113**
Occip.	18	21·37	2·74	7	18·57	0·20	4·361**
(d) bulla—							
L ..	18	12·20	1·61	7	10·64	0·20	3·142**
B	18	8·83	0·28	7	8·37	0·09	2·151*
(e) vacuities							
A.P. vac. L.	17	6·39	0·72	7	6·34	0·35	0·141n.s.
P.P. vac. L.	17	6·81	0·58	8	6·46	0·76	1·024n.s.
P.P. vac. B.	18	9·75	1·00	8	9·16	0·91	1·407n.s.
Mandible—							
Max. L.	17	64·47	20·75	8	57·03	13·58	4·027**
Ramus L.	18	14·52	2·00	8	12·03	1·41	4·334**
Br. at M_2	18	4·81	0·19	8	3·91	0·13	5·099**
Ht. at M_2	18	7·56	0·62	8	6·41	0·39	3·639**
Ramus Angle	18	74·38	11·19	8	77·87	3·26	2·756*

Significance levels :
t Test : ** — 1% : * — 5% : n.s. — not significant.

available specimens adequate for subspecific separation. Thus, and because of the overall small number of specimens, the only statistics of *I. obesulus* included in the present paper (Table 7) are the combined male and female mean values and variances for the species as a whole (as enumerated in Materials and Methods above) for the various dimensions used in the discriminant analysis.

Comparisons of the figures in these seven tables with those in the previous papers on *Perameles* (Freedman, 1967 and Freedman and Joffe, 1967a and b), confirm the various size interrelationships already noted above in the morphological comparisons. Numerous other differences for particular dimensions also become apparent. Those related to sexual dimorphism are dealt with below; others will be discussed later in the course of analysing the discriminant functions.

With regard to sexual dimorphism in the metrical features studied, the "t" values included in Tables 1-3 indicate that, in *I. m. torosus,* for the majority of the cranial dimensions (22/28) and for over half of the dental measurements (upper teeth: 14/26; lower teeth: 14/25) the differences are significant at the 5% level, and in most of these instances significance is actually at the 1% level. On the other hand, the corresponding numbers of significant differences between the sexes in *I. m. macrourus* (Tables 4-6) are very small (cranial: 3/28; upper teeth 5/26; lower teeth: 6/25).

TABLE 2

Comparison of Isoodon m. torosus *male and female upper tooth measurements (in mm)*

Measurement	Males			Females			" t "
	N	X	VAR.	N	X	VAR.	
P^1-M^4	17	45·20	5·37	8	41·35	6·50	3·756**
P^1-P^4	17	6·45	0·20	10	6·01	0·10	2·726*
C^1-M^4	19	34·30	4·99	8	31·08	3·44	3·579**
M^1-M^4	20	17·19	0·93	8	15·97	0·71	3·125**
I^5 L ..	24	1·68	0·03	12	1·50	0·02	3·111**
C^1 L	19	4·20	0·56	10	2·35	0·11	7·395**
B	19	2·12	0·09	10	1·32	0·02	7·930**
H ..	19	6·44	1·99	8	3·56	0·29	5·553**
P^1 L	24	2·81	0·04	13	2·80	0·04	0·145n.s.
B	24	1·30	0·01	13	1·25	0·01	1·451n.s.
P^2 L	24	2·95	0·02	13	3·04	0·009	2·051*
B	25	1·68	0·009	12	1·60	0·04	1·663n.s.
P^3 L ..	22	3·71	0·13	8	3·35	0·04	2·659*
B	22	2·80	0·03	8	2·65	0·04	2·015n.s.
M^1 B ...	25	3·73	0·03	14	3·65	0·06	1·190n.s.
LB ..	25	4·25	0·06	14	4·22	0·05	0·378n.s.
LL	24	3·19	0·08	14	3·15	0·06	0·440n.s.
M^2 B ...	25	4·36	0·11	14	4·27	0·10	0·826n.s.
LB	25	4·26	0·06	14	4·23	0·03	0·404n.s.
LL ...	25	3·50	0·07	14	3·50	0·08	0·000n.s.
M^3 B ..	24	4·77	0·16	9	4·75	0·17	0·126n.s.
LB .	24	4·91	0·11	9	4·65	0·14	1·938n.s.
LL ...	24	4·02	0·07	9	3·74	0·09	2·612*
M^4 B ..	20	3·74	0·06	8	3·46	0·02	3·016**
LB	20	4·82	0·08	8	4·17	0·06	5·688**
LL ..	19	2·40	0·05	8	2·17	0·04	2·511*

Significance levels :
t—Test : ** 1% : * — 5% ; n.s. — not significant.

TABLE 3

Comparison of Isoodon m. torosus *male and female lower tooth measurement (in mm)*

Measurement	Males			Females			" t "
	N	X	VAR.	N	X	VAR.	
I_1-M_1 ..	16	43·02	6·21	9	40·04	6·86	2·819**
I_1-I_3 ...	19	5·20	0·29	12	5·13	0·13	0·396n.s.
$\bar{C}-M_4$	20	36·06	6·46	9	32·90	4·80	3·222**
M_1-M_4	22	18·32	0·77	9	17·42	0·78	2·587*
C L ...	19	3·60	0·44	9	2·34	0·13	5·304**
B	19	2·00	0·08	9	1·26	0·01	7·563**
H ..	18	4·95	0·95	8	2·70	0·18	6·217**
P_1 L	24	2·99	0·72	14	2·98	0·04	0·043n.s.
B ..	24	1·13	0·004	14	1·08	0·003	2·464*
P_2 L	24	3·16	0·03	14	3·15	0·02	0·183n.s.
B	24	1·44	0·01	14	1·33	0·01	3·270**
P_3 L	21	3·60	0·08	9	3·45	0·02	1·501n.s.
B	22	2·01	0·02	9	1·91	0·02	1·787n.s.
M_1 BM ...	22	2·53	0·02	14	2·40	0·04	2·286*
BD	22	3·01	0·03	14	2·86	0·07	2·061*
L	23	3·91	0·06	14	3·73	0·07	2·103*
M_2 BM	25	3·02	0·02	14	2·96	0·07	0·927n.s.
BD	25	3·53	0·07	14	3·27	0·13	2·580*
L ..	25	4·28	0·08	14	4·29	0·06	0·110n.s.
M_3 BM	25	3·32	0·04	14	3·22	0·06	1·381n.s.
BD	25	3·44	0·08	13	3·30	0·09	1·418n.s.
L	25	4·61	0·09	13	4·60	0·08	0·099n.s.
M_4 BM	22	3·14	0·03	9	3·07	0·05	0·938n.s.
BD ..	22	2·55	0·04	9	2·18	0·02	5·035**
L	22	5·55	0·07	9	5·14	0·02	4·370**

Significance levels :
t Test : ** = 1% : * = 5% ; n.s. — not significant.

in *I. macrourus* and so are the very small I^1 teeth. In the small sample available sexual dimorphism was not detected.

(c) *I. barrowensis*:—The single male *I. barrowensis* individual is very similar to the *I. obesulus* specimens in morphology, but, on size, it appeared to be slightly smaller. Because only this one specimen is currently available, no further comments on the morphology seem appropriate.

In a recent paper analysing fossil bandicoots from Mammoth Cave, Western Australia, Merrilees (1967) has listed a series of features useful for distinguishing the genera *Macrotis*, *Isoodon*, *Perameles* and *Chaeropus*. With regard to *Isoodon* and *Perameles*, the present study confirms and extends the shape differences in the muzzle, mandible and molar teeth listed by Merrilees and also describes certain other important differences. The only point of major disagreement between the two studies relates to the alisphenoid bulla. Merrilees describes these as being large in both *Isoodon* and *Perameles*, although differing in shape. As stated in ships differ in the two sexes and these are not treated separately in the table. In the same the text and illustrated in photographs in 2 previous studies (Freedman, 1967; Freedman and Joffe, 1967b) the bulla is relatively small in *P. nasuta*, *P. gunnii* and *P. b. bougainville* and only of comparable relative size to that of *Isoodon* in *P. b. notina*. The relationship difference between the first premolar and the adjacent canine tooth, which this author discusses, is difficult to evaluate, mainly because the relation- paper, Merrilees gives a most useful table of tooth alveoli dimensions for the 4 bandicoot genera. These will not be discussed below as they are not strictly comparable to the actual tooth dimensions recorded in the present study.

Analysis of Isoodon metrical features

Univariate comparisons

The means and variances, in the males and females separately, for the cranial and dental features studied in *I. m. torosus* and *I. m. macrourus* are listed in Tables 1-6. Study of the individual measurements in the males and females of *I. obesulus* did not indicate any obvious sexual dimorphism in the features which were to be used for the discriminant analysis. Nor, as pointed out above, were the numbers of the

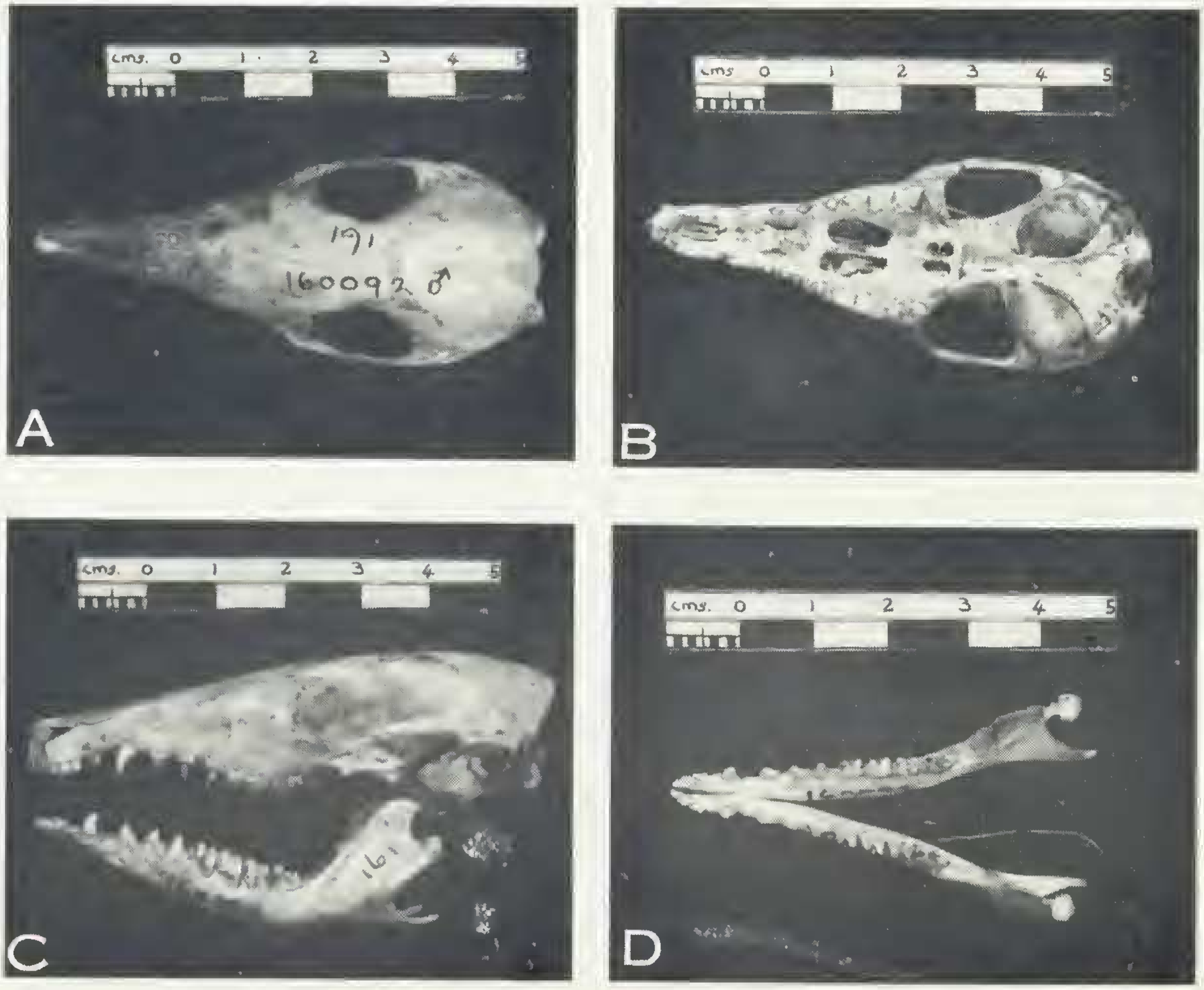

Figure 3.—*Isoodon obesulus affinis* male (Amer. Mus. Nat. Hist. No. 160092). A.—dorsal view of cranium; B.—ventral view of cranium; C.—lateral view of cranium and mandible; D.—occlusal view of mandible.

TABLE 4

Comparison of Isoodon m. macrourus *male and female skull measurements (in mm)*

Measurement	Males			Females			" t "
	N	$\bar{X}$	VAR.	N	$\bar{X}$	VAR.	
Cranium							
(a) length							
Max.	14	75·86	30·24	4	70·77	3·48	1·787n.s.
Bas.	12	68·70	23·00	4	65·12	2·32	1·438n.s.
Cond.-Bas.	12	72·17	23·55	4	68·72	2·05	1·372n.s.
Pal.	12	44·40	9·02	4	42·95	1·03	0·929n.s.
Nas.	11	30·20	7·35	5	28·58	4·58	1·172n.s.
Fr.	14	23·58	2·58	4	21·92	1·36	1·909n.s.
Par.	14	19·65	4·26	4	16·95	1·80	2·443*
Ant. to I^1	13	2·00	0·04	5	1·90	0·02	1·015n.s.
(b) breadth							
Ant. to C	13	8·56	0·69	5	7·70	0·08	2·229*
at M^2	13	21·78	2·52	5	20·36	0·12	1·947n.s.
Int.-Orb.	13	20·53	3·06	5	19·36	0·57	1·424n.s.
Min. Fr.	13	11·27	0·29	4	11·67	0·80	1·117n.s.
Bizyg.	12	33·47	6·34	4	31·25	0·30	1·711n.s.
Cran.	12	25·98	7·67	4	23·62	1·06	1·634n.s.
(c) height							
Ant. to C	13	6·26	0·40	5	5·76	0·14	1·641n.s.
Post. to M^4	12	19·01	1·24	4	18·12	0·08	1·548n.s.
Cran.	12	25·85	3·09	4	24·52	0·61	1·440n.s.
Occip.	12	19·75	2·72	4	17·95	0·07	2·125n.s.
(d) bulla							
L	14	11·80	0·95	4	11·87	0·05	0·139n.s.
B	14	9·18	0·25	5	8·84	0·06	1·440n.s.
(e) vacuities							
A.P. vac. L.	12	5·86	0·40	5	6·12	0·03	0·889n.s.
P.P. vac. L.	13	5·33	0·88	5	5·68	0·21	0·787n.s.
P.P. vac. B.	13	8·43	1·39	5	8·52	0·38	0·160n.s.
Mandible							
Max. L.	13	57·00	14·98	5	54·12	2·02	1·597n.s.
Ramus L.	13	12·76	1·49	5	11·36	0·16	2·472*
Br. at M$_2$	13	4·13	0·15	5	3·82	0·05	1·666n.s.
Ht. at M$_2$	12	7·32	0·91	5	6·48	0·14	1·879n.s.
Ramus Angle	13	78·00	6·00	5	78·60	4·80	0·477n.s.

Significance levels :
t Test : ** 1% ; * 5% ; n.s. not significant.

The subspecific status of I. m. macrourus *and* I. m. torosus

An attempt was next made to investigate the subspecific validity of *I. m. torosus* and *I. m. macrourus*. Because of the marked size sexual dimorphism found in *I. m. torosus* it was considered necessary to treat the sexes separately in investigating the two subspecies. The analysis was made by computing a discriminant function on 27 cranial features to maximise the difference between the males of the two subspecies. The computed function gave a mean score of -27.706 for *I. m. torosus* males (N = 18) and -22.649 for *I. m. macrourus* males (N = 13). Using a sectioning point of -25.177, 3 *I. m. torosus* males fell on the *I. m. macrourus* side of the total distribution, and 3 *I. m. macrourus* males were included on the *I. m. torosus* side.

As a measure of the subspecific validity of the two samples, this test does not meet a stringent application of the 75% rule (i.e. that a subspecies is valid if 75% of the individuals differ from all (= 97%) of a previous subspecies—Mayr, 1969, p. 190). For the discriminant function computed, if a sectioning point is drawn to include *all I. m. macrourus*, 7 out of 18 *I. m. torosus* are included in the *I. m. macrourus* section, i.e. only 61% are excluded. Done in reverse fashion, only 2 out of 13 *I. m. macrourus* are *not* included in the *I. m. torosus* category. However, as this test only involves certain cranial characters, and many other sorts of features can

TABLE 5

Comparison of Isoodon m. macrourus *male and female upper tooth measurements (in mm)*

Measurement	Males			Females			" t "
	N	$\bar{X}$	VAR.	N	$\bar{X}$	VAR.	
I^1–M^4	14	40·13	3·96	5	38·88	1·56	1·302n.s.
I^1–I^4	14	5·63	0·08	5	5·48	0·03	1·102n.s.
C^1 M^4	14	31·62	2·63	6	30·03	1·23	2·176*
M^1 M^4	14	15·48	0·37	6	16·05	0·72	1·708n.s.
I^5 L	15	1·31	0·02	8	1·28	0·01	0·530n.s.
C^1 L	13	4·34	1·61	8	2·06	0·03	5·004**
B	14	1·90	0·10	8	1·21	0·01	5·948**
H	13	5·16	0·96	7	3·35	0·13	4·670**
P^1 L	15	2·62	0·03	9	2·57	0·02	0·730n.s.
B	15	1·22	0·004	9	1·18	0·006	1·379n.s.
P^2 L	15	2·62	0·04	9	2·66	0·02	0·524n.s.
B	15	1·60	0·01	9	1·58	0·03	0·360n.s.
P^3 L	13	3·30	0·14	8	3·00	0·06	2·008n.s.
B	14	2·65	0·03	8	2·68	0·02	0·415n.s.
M^1 B	16	3·67	0·03	9	3·67	0·02	0·000n.s.
LB	16	3·84	0·03	9	3·76	0·04	1·049n.s.
LL	16	2·81	0·09	9	2·85	0·01	0·385n.s.
M^2 B	15	4·38	0·18	9	4·07	0·07	1·964n.s.
LB	16	3·95	0·02	9	3·90	0·02	0·848n.s.
LL	15	3·18	0·15	9	3·13	0·03	0·363n.s.
M^3 B	14	4·82	0·26	8	4·31	0·10	2·547*
LB	14	4·30	0·03	8	4·21	0·07	0·968n.s.
LL	14	3·46	0·05	8	3·41	0·03	0·544n.s.
M^4 B	14	3·67	0·09	7	3·41	0·08	1·905n.s.
LB	14	4·44	0·07	7	4·35	0·08	0·718n.s.
LL	14	2·24	0·03	7	2·27	0·05	0·340n.s.

Significance levels :
t = Test : ** 1% ; * = 5% ; n.s. = not significant.

TABLE 6

Comparison of Isoodon m. macrourus *male and female lower teeth measurements (in mm)*

Measurement	Males			Females			" t "
	N	X	VAR.	N	$\bar{X}$	VAR.	
I$_1$ M$_4$	13	38·87	3·09	5	38·04	0·98	0·985n.s.
I$_1$ I$_3$	12	4·74	0·04	5	4·62	0·15	0·856n.s.
C –M$_1$	13	33·09	2·37	5	31·52	0·43	2·173*
M$_1$–M$_4$	13	16·50	0·28	6	16·63	0·10	0·552n.s.
C L	13	3·46	0·93	8	1·91	0·01	4·486**
B	13	1·76	0·10	8	1·12	0·01	5·422**
H	13	4·10	0·34	8	2·51	0·10	7·054**
P$_1$ L	15	2·73	0·03	8	2·70	0·01	0·448n.s.
B	15	1·04	0·005	8	1·02	0·002	0·722n.s.
P$_2$ L	15	2·94	0·01	8	2·90	0·02	0·791n.s.
B	15	1·35	0·008	8	1·36	0·01	0·245n.s.
P$_3$ L	13	3·15	0·04	8	3·20	0·05	0·532n.s.
B	13	1·85	0·03	8	1·81	0·02	0·548n.s.
M$_1$ BM	15	2·33	0·02	9	2·32	0·01	0·185n.s.
BD	15	2·76	0·02	9	2·74	0·04	0·287n.s.
L	15	3·56	0·03	9	3·46	0·02	1·460n.s.
M$_2$ BM	14	2·92	0·03	9	2·83	0·02	1·301n.s.
BD	14	3·49	0·16	9	3·21	0·08	1·820n.s.
L	14	3·99	0·04	9	3·95	0·02	0·520n.s.
M$_3$ BM	15	3·18	0·07	9	3·00	0·01	1·944n.s.
BD	15	3·44	0·20	9	3·03	0·07	2·488*
L	15	4·16	0·06	9	4·28	0·05	1·198n.s.
M$_4$ BM	13	3·05	0·08	8	2·85	0·05	1·695n.s.
BD	13	2·57	0·05	8	2·22	0·03	3·772**
L	13	5·03	0·07	8	5·07	0·05	0·355n.s.

Significance levels :
t Test : ** 1% ; * = 5% ; n.s. - not significant.

be utilised in taxonomy, especially at the subspecific levels, no final conclusion can be drawn as to the validity of the two subspecies.

Interrelationships within and between Isoodon *and* Perameles

In order to investigate further the interrelationships within the genus *Isoodon*, and also to provide an over-all comparison of these taxa with others of the genus *Perameles*, both grouped and ungrouped specimens of the two genera (see Table 8) were included in multiple discriminant analyses. The first analysis made was based on 26 variates measured for the cranium and mandible; the second trial utilized 23 dimensions of the premolar and molar teeth.

TABLE 7

Means and Variances (in mm) for (combined male and female) Isoodon obesulus *measurements Used in Discriminant Analysis*

Measurement	$\bar{X}$	VAR.	Measurement		X	VAR.
Cranium—(N 10)			Upper teeth (N 14)			
(a) length			P^1	L	2·31	0·02
Max.	62·52	40·96		B	1·04	0·02
Bas.	57·90	33·40	P^2	L	2·37	0·03
Cond.-Bas.	60·78	37·08		B	1·27	0·01
Pal.	37·40	15·21	M^1	B	2·83	0·04
Nas.	25·63	12·25		LB	3·22	0·16
Fr.	21·13	2·95		LL	2·54	0·07
Par.	14·23	2·68	M^2	B	3·27	0·04
(b) breadth				LB	3·37	0·12
Ant. to C	6·72	0·20		LL	2·75	0·10
at M^2	17·39	1·23	Lower teeth (N 14)			
Int.-Orb.	18·96	1·98	P_1	L	2·43	0·05
Min. Fr.	12·01	0·46		B	0·91	0·01
Bizyg.	27·81	3·42	P_2	L	2·67	0·05
Cran.	23·10	2·85		B	1·10	0·01
(c) height			M_1	BM	1·81	0·03
Ant. to C	5·54	0·30		BD	2·21	0·03
Post to M^4	15·64	1·29		L	3·10	0·06
Cran.	22·28	4·28	M_2	BM	2·23	0·03
Occip.	16·06	2·22		BD	2·57	0·01
(d) bulla				L	3·36	0·07
L	10·35	0·43	M_3	BM	2·38	0·04
B	8·29	0·18		BD	2·55	0·02
(e) vacuities				L	3·57	0·15
A.P. vac. L	4·96	0·06	Mandible (N 10)			
P.P. vac. L	7·17	1·21	Max. L		48·14	22·37
P.P. vac. B	7·41	0·65	Ramus L		8·51	0·72
			Br. at M_2		3·27	0·13
			Ht. at M_2		5·04	0·28

TABLE 8

Numbers of Specimens used in Discriminant Analyses

Group	Adults (Skull Analysis)	Adults and Juveniles (Tooth Analysis)
Isoodon m. torosus males	18	24
Isoodon m. torosus females	7*	14
Isoodon m. macrourus males	13	15
Isoodon m. macrourus females	4*	9
Isoodon obesulus (males and females)	10	14
Perameles nasuta males	36	49
Perameles nasuta females	32	53
Perameles gunnii males	19	23
Perameles gunnii females	18	25
Perameles b. notina (males and females)	12	16
Perameles b. bougainville (males and females)	5*	9
Total	174	251

* Run as unclassified individuals to be scored after computation of the discriminent weights.

Multivariate analysis of this type allows several groups or populations to be dealt with simultaneously. The technique also permits considerable reduction in the dimensionality of the space in which these groups are treated, from a figure equal to the number of original measurements to a maximum of one less than the number of groups employed (here 8 minus 1 for the skull analysis and 11 minus 1 for the tooth trial). Further, in this reduction to a "discriminant space," there is often little loss of total "information"; i.e. the configuration of groups as plotted on several discriminant functions or axes in the reduced space is not likely to be very different from that obtaining in the original space of greater dimensionality. Often only the first two or three functions computed are necessary to construct a space in which the essential nature of group interrelationships is retained.

(a) *Skull analysis:*—The analysis of 26 measurements of the cranium and mandible taken on eight taxonomic groups of *Isoodon* and *Perameles* would be expected to yield a maximum of seven discriminant functions. However, the first five axes computed are sufficient to account for over 99% of total discrimination and, of this battery, the first two discriminants are most important, contributing 70.8% and 22.6% of total separation, respectively.

Using the first two functions, group centroids for the 8 taxa studied (and 95% probability ellipses to illustrate dispersion for *P. nasuta* males and females) are plotted in Figure 4. It is apparent that considerable separation of the groups in the discriminant space has been achieved. Chi-square output (relating each of the 158 grouped specimens to each of the centroids) was computed according to the procedure outlined in Cooley and Lohnes (1962, pp. 135-136). The results indicate that in fact over 83% (133/158) of cases have been *assigned* correctly, i.e. lie closer in terms of chi-square "distance" to their own group centroid than to any other. And of the 25/158 misassignments noted, 21 are by sex within species, and four are to the incorrect subspecies (e.g. to *I. m. torosus* rather than to *I. m. macrourus*, or vice versa); no specimens are misassigned at the species or genus level.

These chi-square values can also be used to assess *classification* of individuals in absolute terms, meaning the extent to which specimens fall within their own expected population distributions and are at the same time excluded from other distributions at some chosen level of probability. Here again, all skulls are excluded at 95% probability from membership in the incorrect species (or genus), though many are not excluded as belonging to the incorrect sex, or subspecies in the case of *I. macrourus*. Only three individuals, correctly excluded from all inappropriate groups, also all beyond the 5% limits of their own distributions as well; these last may be said to be misclassified.

When the several ungrouped specimens (whose measurements were not used in computing the functions) are considered, *I. m. torosus* and

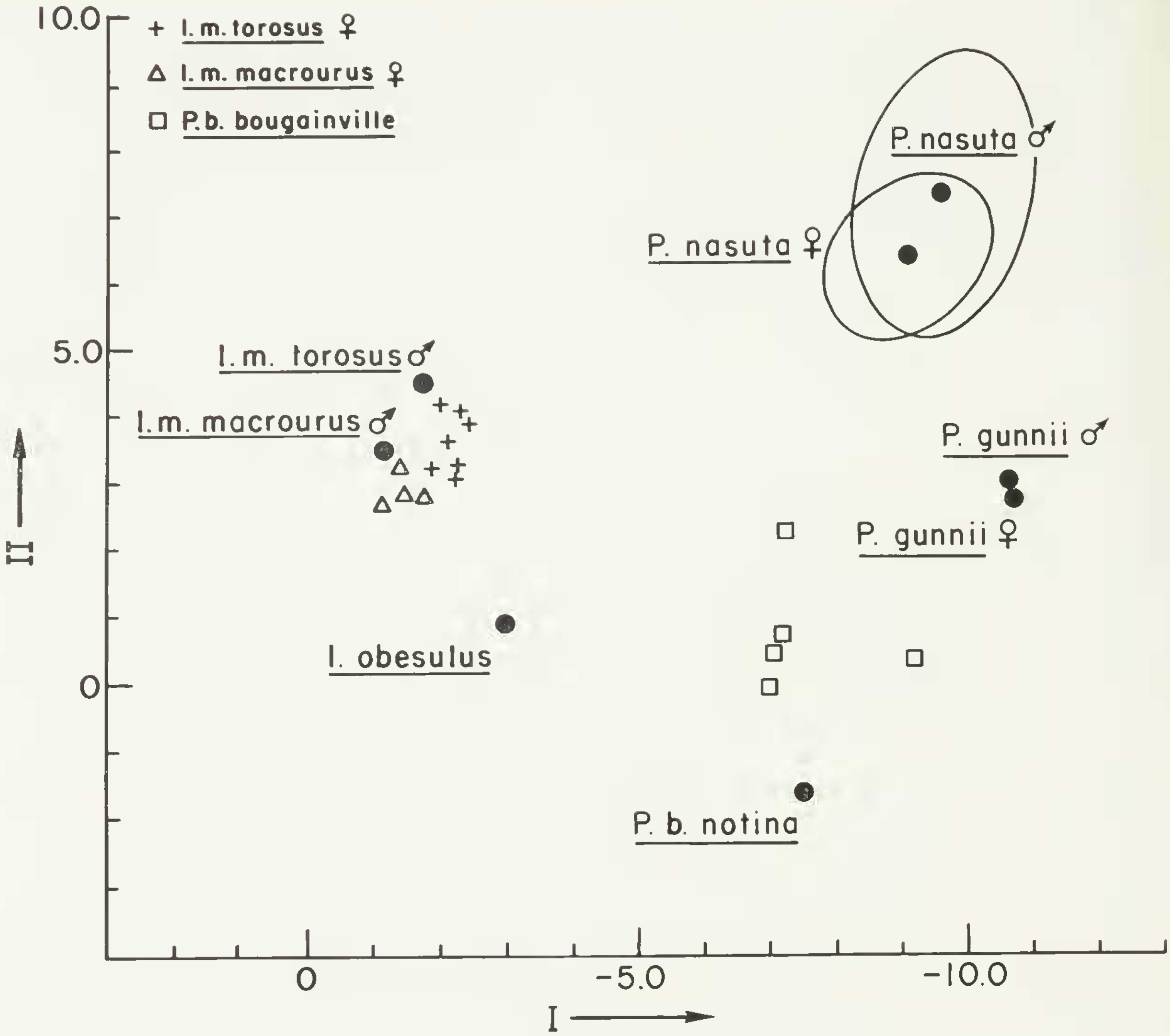

Figure 4.—*Isoodon* and *Perameles* group centroids and individual scores on functions I and II computed from 26 skull measurements; 95% contours illustrating expected dispersions for *P. nasuta* males and females are included.

I. m. macrourus females are seen to lie close to the respective male centroids in the figure, and chi-square data show that, as expected, all are excluded at 95% probability from any save *I. macrourus* distributions. *Perameles bougainville bougainville* individuals, numbering five, are uniformly excluded at 95% probability from all groups, *P. b. notina* included.

Further examination of the centroids plotted in Figure 4 suggests that function I is operating primarily to distinguish *Isoodon* populations from those of *Perameles*, i.e. that this most important contributor to over-all group separation is picking up differences which are of a generic nature. *I. m. macrourus, I. m. torosus* and *I. obesulus* tend toward considerably higher (less negative) mean scores (-1.18, -1.77 and -2.99 respectively) on this axis than do the several *Perameles* species, which range between -7.55 *(P. b notina)* and -10.74 *(P. gunnii* females) on the same scale. Intrageneric distinctions, either by species (or subspecies) or by sex where males and females have been grouped separately, are not especially apparent.

The relative importance of individual variates to the discrimination afforded by this function may be assessed by reference to the associated scaled vector (Table 9). The elements of the vector correspond to the discriminant weights, but are re-scaled to allow for differences in measurement size and are thus directly comparable (whereas the weights alone are not). Basal length of the skull and inter-orbital breadth seem quite prominent here, the latter receiving the greatest scaled weight of all 26 variables included in the analysis. The negative sign of this weight is as expected, since *Isoodon* species have generally smaller inter-orbital breadths and so should tend toward less negative scores than the *Perameles* groups, as in fact observed. Another significant discriminator is mandibular ramus length, which is weighted

TABLE 9

First and Second Discriminants Computed in an 8-group Analysis Using 26 Measurements of the Skull

Measurements	Weights		Scaled Weights		F-
	Function I	Function II	Function I	Function II	Ratios*
Max. length	—0·038	—0·068	—2·206	—3·953	78·99
Bas. length	—0·083	0·141	—4·081	6·872	90·70
Cond.—Bas. length	—0·022	0·046	—1·133	2·318	90·19
Pal. length ...	0·084	0·309	2·583	9·478	125·46
Nas. length	—0·036	0·017	—0·999	0·466	93·83
Fr. length	0·009	—0·030	0·205	—0·659	30·16
Par. length	—0·015	—0·039	—0·284	—0·724	90·45
Breadth ant. to C	0·044	0·091	0·322	0·663	68·57
Breadth at M^2	0·035	0·120	0·559	1·910	74·82
Int.—Orb.	—0·417	—0·317	—6·171	—4·682	77·57
Min. Fr. breadth	0·157	—0·041	—1·079	—0·280	102·40
Bizyg. breadth	0·083	—0·052	1·817	—1·155	75·95
Cran. breadth	—0·006	—0·152	—0·139	3·285	29·46
Height ant. to C	0·047	0·135	0·273	0·785	69·14
Height post. to M^4	0·165	0·417	1·528	3·859	118·02
Cran. height ...	0·103	—0·221	1·622	—3·479	61·64
Occip. height	—0·087	0·035	1·261	0·500	63·00
Bulla length ..	0·211	—0·458	1·722	—3·737	382·52
Bulla breadth	0·337	—0·115	1·515	—0·517	224·87
A.P. vac. length	—0·131	—0·205	—1·101	—1·723	115·27
P.P. vac. length	—0·119	—0·148	—1·271	—1·580	37·22
P.P. vac. breadth	0·000	—0·190	0·002	—2·049	23·38
Mandible length	—0·009	0·061	0·377	2·553	90·96
Ramus length	0·470	0·147	4·983	1·553	245·46
Breadth at M_2	0·006	0·175	0·025	0·736	103·55
Height at M_2 ...	—0·139	—0·084	—1·152	—0·693	51·52

* Degrees of freedom are 7 and 150.

positively in keeping with the markedly greater values which this variate assumes in the several *Isoodon* (particularly *I. macrourus*) populations measured. Several other measurements, including maximum skull length, palatal length, bizygomatic breadth, cranial height taken posterior to M^1 and from basion to bregma, and length and breadth dimensions of the alisphenoid bulla, also seem important but contribute somewhat less than the aforementioned.

Function II, accounting for only 22.6% of total variance, is evidently operating rather differently. Generic distinctions are here lost completely, as the *Isoodon* taxa have mean scores which lie well within (actually toward the centre of) the range of scores received by the three *Perameles* species represented. However, the *I. obesulus* and *I. macrourus* groups are clearly separated, and the *P. nasuta, P. gunnii* and *P. bougainville* populations are also mutually distinct from one another, so that differences *within* each genus seem to be considerably more apparent on this axis than on function I. Separation by sex is again minor, but the distribution of groups does suggest that "size" is here a factor in discrimination, since the smaller more delicately constructed species (*I. obesulus* and *P. bougainville*) tend to receive low scores and the observed size/robusticity sequence within *Perameles* (*P. nasuta* > *P. gunnii* > *P. bougainville*) is in fact reflected on this discriminant scale.

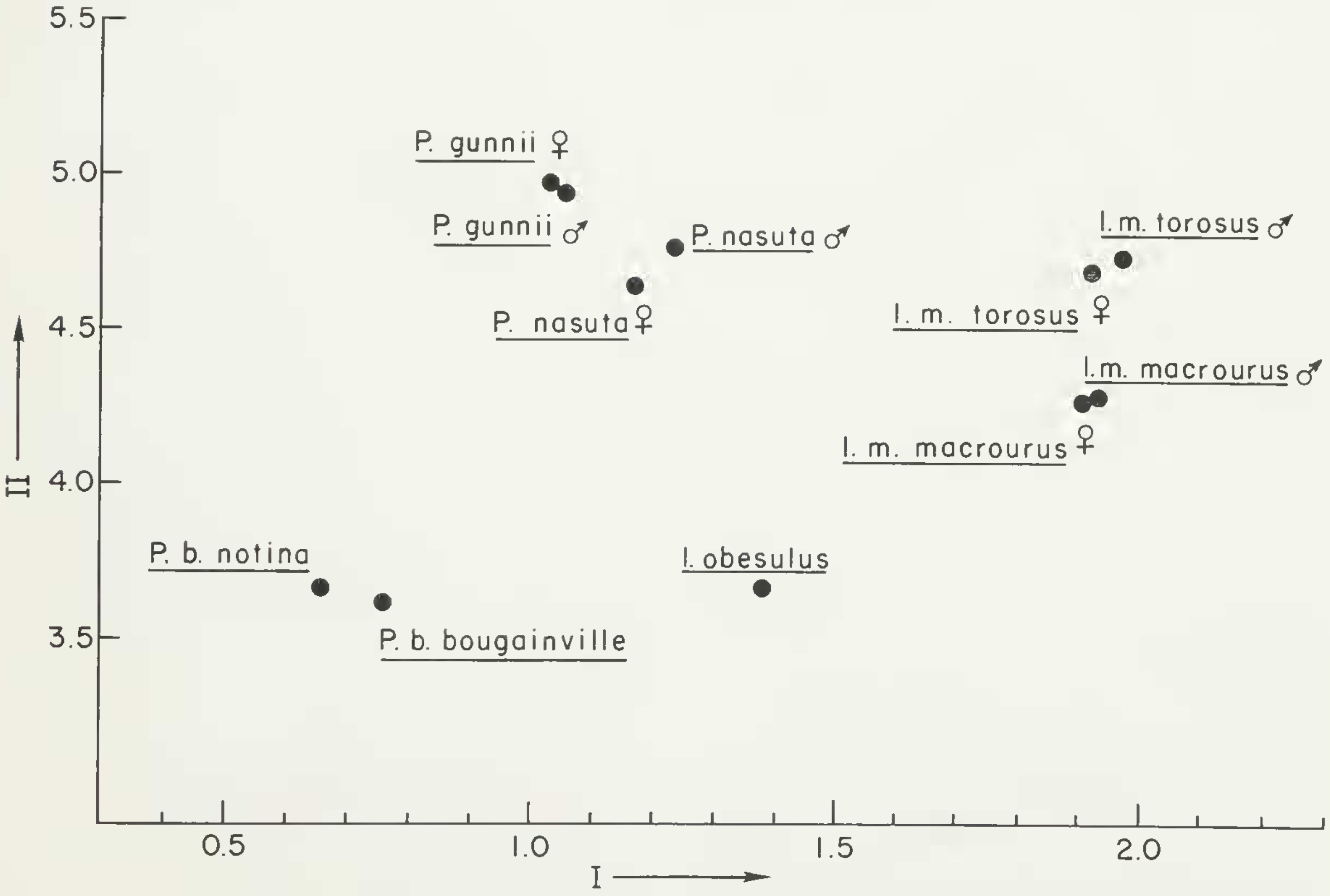

Figure 5.—*Isoodon* and *Perameles* group centroids on functions I and II computed from 23 tooth measurements.

Judging from the scaled weights (Table 9), palatal length and basal skull length are the two variates contributing most heavily to discrimination along axis II, and both are weighted positively. These dimensions are greatest for *P. nasuta* (males and females), smallest in *P. bougainville* and *I. obesulus*, and seem to be good size indicators, so that this weighting is not unexpected. Certain measurements previously seen to be important on function I (e.g. maximum skull length, inter-orbital breadth, cranial height, and bulla length) are also significant here, but others such as ramus length and bizygomatic breadth are de-emphasised, and this second scaled vector is certainly not coincident with the first; this again suggests that the roles played by the several variables are not the same and that discrimination along these axes is effected in rather different ways.

(b) *Dental analysis:*—Owing to the increased sample sizes resulting from the inclusion of certain juvenile specimens, 11 groups of bandicoots could be treated in a discriminant analysis based on premolar and molar tooth measurements. Computation yields a total of ten discriminant functions, each a linear compound of the 23 original variates, but the first seven of these provide more than 99% of overall group separation; functions I and II alone account for some 87% of discrimination, and group centroids on these axes are illustrated in Figure 5.

Inspection of this figure reveals a configuration of groups which is generally similar to that obtained using measurements of the skull, and the level of discrimination achieved is also about the same. Assignments as read from the 11 chi-square values computed for each of the 251 specimens run are correct in 82% (206/251) of cases, and the 45 misassignments recorded are by sex only. Thus in one sense discrimination is actually better here than in the skull analysis, since in fact no individuals are assigned to the inappropriate taxon, even at the level of the subspecies. In absolute terms, all but seven skulls (*P. nasuta* or *P. gunnii*) are correctly excluded at 95% probability from the inappropriate species, though many lie within the territory of a neighbouring (incorrect) sex or subspecies. Eleven specimens are actually misclassified, i.e. lie beyond the 5% limits of their *own* groups.

The distribution of group mean scores on axis I indicates that, despite the proximity of *P. nasuta* males to *Isoodon obesulus*, this first and most important function is acting to separate taxa of *Perameles* from those of *Isoodon* and is thus again discriminating genera. However, this (generic) separation is not as clear as in the skull-based analysis, and it seems likely that *I. obesulus* at least is rather less easily distinguished from species of *Perameles* on dental criteria than by reference to the cranium and mandible.

The listing of scaled weights for this function (Table 10) shows that length measurements of certain molars (M^1, M^2 and M_2) and of P_2 are the more significant contributors to discrimination, whereas dimensions of the other premolars and molar breadths (with the exception of mesial breadth of M_3) have relatively minor roles. Of the former, M^2 lingual length, and M_3 mesial breadth, both weighted positively, are consistently greater in average value in populations of *Isoodon*, so that these groups tend to have the higher scores. Other variables, which are not such good discriminators at the generic level when considered alone, are evidently acting in combination to effect group separation, but interpretation of these aspects of measurement co-variation is difficult.

TABLE 10

First and Second Discriminants Computed in an 11-group Analysis Using 23 Tooth Measurements

Measurements		Weights		Scaled Weights		
		Function I	Function II	Function I	Function II	F-Ratios*
P^1	L	0·091	0·276	0·210	0·635	35·78
P^1	B	−0·071	−0·126	0·109	0·195	44·35
P^2	L	−0·045	0·117	−0·095	0·250	50·31
P^2	B	0·060	0·019	0·107	0·034	52·16
M^1	B	0·208	0·145	0·446	0·311	191·91
M^1	LB	−0·217	0·385	0·867	1·535	63·02
M^1	LL	−0·016	0·054	−0·051	0·171	49·79
M^2	B	0·113	0·070	0·359	0·224	138·80
M^2	LB	−0·097	0·220	0·337	0·764	64·70
M^2	LL	0·252	−0·252	0·762	−0·762	96·12
P_1	L	−0·121	−0·207	−0·299	−0·512	20·23
P_1	B	0·181	0·034	0·179	0·033	53·91
P_2	L	−0·330	0·170	0·737	0·378	37·23
P_2	B	0·069	0·228	0·096	−0·313	47·10
M_1	BM	0·110	0·344	0·277	0·865	65·76
M_1	BD	0·060	0·176	0·421	1·238	11·28
M_1	L	−0·114	0·009	0·402	0·030	38·34
M_2	BM	0·053	0·068	0·286	0·367	23·18
M_2	BD	0·026	0·043	0·089	0·149	86·34
M_2	L	0·220	0·162	0·689	0·509	79·88
M_3	BM	0·269	0·152	0·591	−0·336	207·10
M_3	BD	0·001	−0·051	0·002	−0·202	69·73
M_3	L	0·133	0·250	0·141	0·829	94·94

* Degrees of freedom are 10 and 240.

If function II is considered alone, the *Isoodon*/*Perameles* dichotomy disappears altogether (as in the analysis of the skull), though certain intrageneric distinctions appear to be sharpened. *I. m. torosus* males and females are here removed somewhat from *I. m. macrourus* and *I. obesulus* is again shown to be clearly different from each; the *P. bougainville* groups lie well apart from the other *Perameles* species, though *P. b. notina* and *P. b. bougainville* continue to cluster together. The principal contributors to discrimination on this axis are buccal length of M^1 and distal breadth of M_1, both weighted positively; and of all the taxa measured, *I. obesulus* and *P. bougainville* are the smallest in these dimensions, which must in large part account for their lower discriminant scores.

The remaining functions (not plotted), which make successively smaller additions to discrimination in other dimensions, appear to alter but little the general configuration of taxa as indicated in Figure 5 and need not be dealt with here.

Conclusions and Summary

The present study of certain taxa of the genus *Isoodon* has quantified and highlighted a number of significant features of the skull and teeth of the group and some of its subdivisions. Notably, *Isoodon* is shown to be characterised relative to *Perameles*, by its broader muzzle, greatly inflated alisphenoid bullae (*P. b. notina* is, however, similar), antero-posteriorly long mandibular rami, small I^1 teeth, broad last premolars and rather squared, compact molars. As in the genus *Perameles*, sexual dimorphism is more apparent in the larger than in the smaller forms. In addition to its value for making taxonomic decisions, with regard to extant populations, the tables of skull and tooth measurements (Tables 1—7), used in conjunction with those previously published (Freedman, 1967 and Freedman and Joffe 1967a and b), should be most useful for identifying and evaluating subfossil and fossil material of the Peramelidae.

The intraspecific analysis of *Isoodon* and the comparisons with *Perameles*, for both of which discriminant analysis was used, have again illustrated the value of this technique for taxonomic studies. On the accepted criteria, the subspecific status of *I. m. macrourus* and *I. m. torosus* could not be unequivocally established solely on the basis of the particular cranial and dental features studied, but the degree of separation achieved in the trial would seem at least to provide important grounds for the full investigation of other characters.

In the 8 group multiple discriminant analysis, based on 26 cranial and mandibular measurements, and in the 11 group analysis, using 23 dental dimensions, the configuration of the *Isoodon* and *Perameles* group centroids is generally similar. However, the skull analysis should provide the more reliable picture of group relationships, as the multiple measurements utilised permit individual skulls to be considered as more meaningful biological entities which can then be dealt with in population terms. In the dental analysis, molar and premolar teeth only are included and it is perhaps surprising, but significant, that the results of this analysis and the one utilizing widespread skull features agree as closely as they do. In both of the above analyses, the first and most important discriminant axis computed serves to separate the *Perameles* taxa from those of *Isoodon;* the additional functions seem to sharpen intrageneric distinctions. This appears to indicate that the generic distinction is here the major one, and that specific or subspecific differences are secondary. Nevertheless, in both analyses *I. obesulus* lies well separated from *I. macrourus* and *P. nasuta* is clearly discriminated from *P. gunnii*. Differentiation of the sexes, where these are treated separately, is always minor and does not appear to be a factor in discrimination.

In both the skull and dental analyses, *P. b. bougainville* and *P. b. notina* lie close together, although in the skull trial the 5 ungrouped *P. b. bougainville* specimens are excluded from *P. b. notina* at 95% probability. With regard to their relationships to *P. gunnii* and *P. nasuta*, in the skull analysis the *P. b. bougainville* specimens lie rather close to the *P. gunnii* centroids (Fig. 4), whereas in the dental analysis the centroids of both *P. bougainville* subspecies are well separated from those of the other two *Perameles* species (Fig. 5). Relying principally on the dental analysis, for which sample sizes are considerably larger and in which *P. b. bougainville* has actually been used in computing the discriminant functions, it seems that the closeness of the centroids for *P. b. bougainville* and *P. b. notina* suggests that the two populations most probably only merit subspecific separation, whilst their clear separation in this test from the other two *Perameles* species appears to validate their specific status as a group.

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